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Parturition and related behavior in wild American beavers *(Castor canadensis)*

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Abstract

Parturition in a family of wild American beavers *(Castor canadensis)* was observed in their natural lodge in two consecutive years. Behavioral and/or morphological characteristics of eight neonates, five yearlings and an adult pair before and during parturition are described and compared with analogous data gathered by other authors on captive beavers. It is shown that while beavers, with respect to parturition, definitely have many traits that are typical of precociality, they also possess a number of characteristics akin to altriciality, both in behavior and morphology.

Introduction

Speaking about Eutherians in her Ethology of Mammals, R. F. Ewer (1968) stated: "In general, if the adult normally occupies a protected lair or burrow, the young are altricial; if there is no such home and the limbs are not adapted to constructing one to cope with the special needs of the young, then they must needs be precocial. This correlation is shown very clearly in the rodents" (p. 245). Beavers, both the American *(Castor canadensis)* and the European *(C. fiber)* species are noticeable exceptions to that rule. According to all accounts found in the literature (references in Djoshkin and Safonow 1972; Jenkins and Busher 1979), beaver kits are born hairy and toothed, and their eyes open at most a few hours after birth: in these respects, they are precocial animals. However, they are born in their parents' protected home (e.g., the beaver lodge), in which they normally remain absolutely confined for 4–5 weeks: in this respect, they are literally "nidicolous" animals, in spite of their precociality. Exceptions are often very useful for understanding general rules. Considering the various correlates of altriciality and precociality (Dieterlen 1963; Ewer 1968), the behavioral study of parturition and ontogeny in beavers might contribute to a better characterization of these strategies in mammals.

The present paper deals with parturition. Incidental indications on behavior related to parturition in beavers are found in Grey Owl (1935), Wilsson (1971), Hirai (1975), Richards (1977), Doboszynska and Zurowski (1982). Shadle (1930) and Hediger (1970) have produced more substantial accounts on the topic. All these papers deal with captive or semi-captive individuals, and the question arises of possible "forcing" effects of keeping conditions on behavior (e.g., nest building or fitting, presence or absence of conspecifics with the mother and her kits, movements of neonates, etc.). The objectives of this paper are to present the results of observations made on parturition in wild American

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beavers, to compare them with observations published by other authors on captive or semi-captive beavers, and to clarify what behavioral characters related to parturition in this "exceptional" genus are altricial or precocial.

For a better understanding of the context in which parturition occurs in the American beaver, the following should be known (references in Djoshkin and Safonow 1972; Jenkins and Busher 1979). Generally speaking, adult beavers form perennial pairs that produce one yearly litter of 3–4 kits. Copulation occurs in January or February, parturition in May. Young beavers stay with their parents until they are about 23 months old, at which time they disperse to form new pairs. Beavers thus live in familial social units that consist of an adult pair and, possibly, one or two successive litters. They all occupy a familial nest that often consists of a typical lodge with underwater entrances.

Material and methods

The observations reported in this paper were made during an intensive research on the behavior of wild beavers, carried out in Gatineau Park, Quebec, Canada (45° 35′ N, 76° 00′ W). Among others, one family was studied continually from June 1976 through September 1978 for a total of 857 hours of observation, and two parturitions were observed in this family on May 26, 1977 and May 19, 1978. Composition of the family on these two days is shown in the Table. The 1977 parturition occurred in the lodge the family inhabited from August 1976 to October 1977, adjacent to the bank of a small isolated, 6 ha lake. The 1978 parturition occurred in another lodge the family had moved into in October 1977, 26 m off the shore of the same lake and 100 m from the first lodge.

Table

Composition of the beaver family on parturition days

Date	Adults ♀	Adults ♂	Yearlings	Kits
May 26, 1977	A	B	C, D	E, F, G, H
May 19, 1978	A	B	E, F, G	I, J, K, L

Prepartum activities as well as parturitions were observed with a special device described by Patenaude-Pilote et al. (1980), allowing direct observations, video-recording and photographing of the beavers inside their lodge. In 1977, between April 1st and parturition day, we made 65.7 hours of observation over 42 days inside the lodge (including 11.0 hours on parturition day itself). In 1978, in an attempt to avoid the disturbances to the female caused by the observer's presence, observations were discontinued in April; from May 1st till May 18, they were limited to a total of 4.1 hours, consisting mostly of short daily sessions; they were carried out for 8.2 hours on parturition day (May 19). The adult female, the adult male, the yearlings and the neonates could be easily identified as such, but individual young of a given age could not always be reliably distinguished from each other, and their sex could not be determined. The presence of many beavers (3 to 8 at a time) inside the small room of the lodge during parturitions, and their brief lived and varied activities made it often difficult to record the exact time and duration of each behavior.

Information on the ossification stage of beaver kits at birth was obtained from radiographs made of four fetuses removed from a gravid female killed by a trapper on May 29, 1980 in Laurentides Park (north of Quebec City). According to their weight (550, 532, 508 and 496 g), and the state of their hair and teeth, they were certainly full-term.

Results

During the weeks preceding parturition

In 1977, from April 14 until the day before parturition, the female consistently avoided staying in the lodge when observations were carried out: she would not enter the lodge as long as the observer was present, or would leave it whenever the observer approached the

observation device, if she happened to be inside at that time. Yearling C, who used to stay with its mother at all times, had the same behavior. As a result, most observations made in the lodge between the middle of April and parturition day in 1977 concern only the male and yearling D. In 1978, however, neither the female nor any other member of the family appeared to be disturbed by the observer's limited presence during the weeks preceding parturition. All beavers could then be regularly seen in the lodge.

Besides the fearful reactions to the observer displayed by the female in 1977, the only activities of this period in both years that were clearly different from the standard year-round routine concerned a peculiar type of fitting-up of the lodge's inner part. In both years, this involved a scraping away of lateral walls of the room, performed with incisors and hands resulting in an increase of its diameter from 130 to 160 cm (thus an increase of about 50 % in surface area). The roof and floor remained untouched. First signs of this activity were observed 52 days before the 1977 parturition, but only 8 days before the 1978 one. In 1978, both adults and each of the three yearlings were seen engaged in it. In 1977, only the male and yearling D were seen scraping the wall. The female and yearling C might have been involved in the observer's absence. In both years, the floor of the room was found covered with fresh herbs two days before parturition. We consider this and the scraping of the wall as parts of prepartum behavior, since we observed them shortly before parturition in another colony, but never in lodges occupied by a non-reproductive pair or a lone individual.

The 24 hours before parturition

On May 25, 1977, at 10.32 (E.S.T.), the female entered the lodge while an observer was "on duty", stayed for 8 minutes and left. Later on that day, observations were carried out from 15.25 to 17.30, and from 19.50 to 20.45. The female was in the lodge at 15.25 and left only 1 hour and 45 minutes later; she was also there at 19.50 and had not left by the end of observations. During her stays in the lodge, she was extremely restless (compared to her own behavior after parturition, as well as to the behavior of other, non-parturient females): she would engage in series of alternating bouts of walking, grooming or resting, each a few seconds in duration. At 16.31, she had some sudden, jerky vertical movements of the tail, similar to those observed the next day in conjunction with contractions associated with deliveries. When observations resumed on May 26 at 05.15, the female was and remained in the lodge with the male and yearling D. Except for a bout of mutual grooming with the male at 06.29, she appeared rather sleepy until 09.10, when the parturition process was initiated by a series of abdominal contractions.

In 1978, on May 18 as well as in the morning of May 19 (parturition day), nothing peculiar in the behavior of the female or of any of the other four beavers was suggestive of an approaching parturition, except for three sudden jerks of the female's tail at 09.58 (May 19), similar to those observed in 1977 18 hours before parturition. Everything was then so quiet in the lodge that the observer left at 10.30, convinced that nothing would happen the same day. When observations resumed at 15.00, two kits were already born . . .

During and after parturition

Four kits were born each year. Five births occurred during observation periods: numbers 1, 3 and 4 in 1977; numbers 3 and 4 in 1978. The chronology of events observed in 1977 and 1978 is shown in Figs. 1 and 2, respectively. These events are described and commented upon below.

Female's behavior

The abdominal contractions were wave-like processes occurring in series, each "wave" lasting about 2–3 sec. They were often accompanied by jerky movements of the tail. While

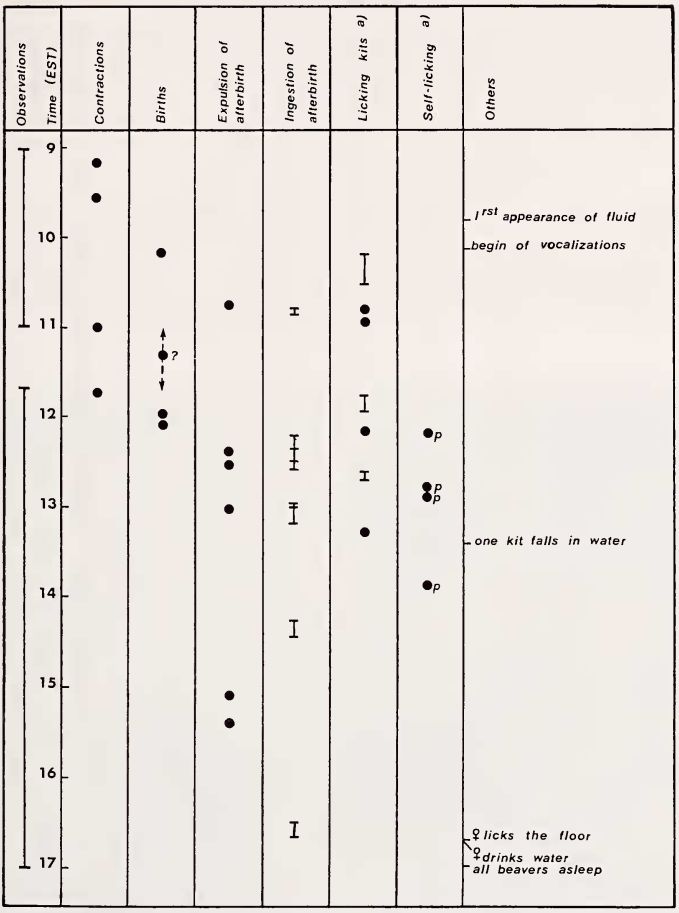

Fig. 1. Major events observed on May 26, 1977. Notes: a) by female; p = pseudo-cloacal area

they occurred, the female was observed in any one of the following positions: lying on the side, the back or the belly, sitting on the haunches, standing on all fours, or curled-up.

In 1977, the first birth was preceded by the female emitting a peculiar moo-like vocalization (heard in that instance only throughout the entire study) and a series of strong and low-pitched whines, which appeared to catch the attention of the male and yearling D (see following section). The first birth of 1978 was not observed. For each of the five births observed, the female adopted the following typical posture: sitting up with the tail stretched forward, head bent down toward the pseudo-cloaca, back arched. At most a few seconds elapsed between the female's assuming this posture and the complete expulsion of the young on the mother's tail. The female never used her hands or teeth in the process. On the two instances that we could clearly see the young emerging from the birth canal, it was head first. The umbilical cord ruptured at expulsion time in all cases. Only one young kept a 3 cm piece of cord still attached, which was eaten 4 hours later by the female.

The afterbirth (composed of placentae, amniotic and chorionic membranes and a large amount of fluid: Kristal 1980), was expelled in numerous parts between and after expulsions of fetuses. During expulsion of parts of afterbirth, including fluid alone, the female's posture and behavior were similar to those displayed while giving birth, except

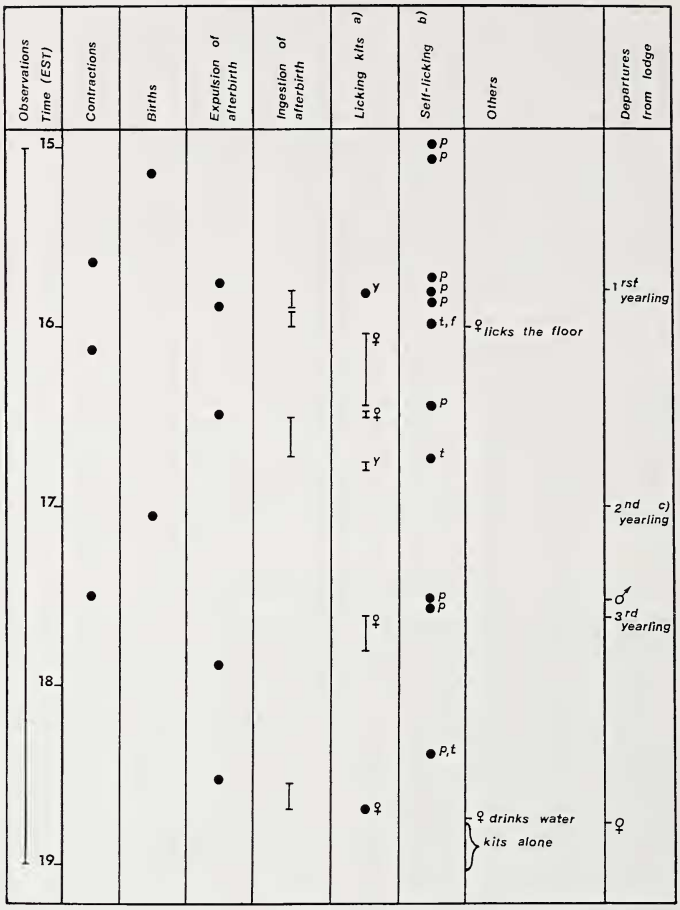

Fig. 2. Major events observed on May 19, 1978. Notes: a) by female (♀) or yearling (Y). b) by female; p = pseudo-cloacal area, t = tail, f = frontpaw. c) final departure: see text

that she made occasional use of her teeth and/or hands to extract fragments from her pseudo-cloaca. The female slowly ate all the pieces of afterbirth (Fig. 3), not necessarily immediately after their expulsion, and was seen on one occasion retching while doing this. In both years, she was seen drinking from the waterhole in the lodge, a few minutes after eating the last piece. This is noteworthy, since these were the only two instances in 819 hours of observation in various lodges throughout the general study that we have seen a beaver drinking water.

During the parturition process, the female spent considerable amounts of time in licking activities (see Figs. 1 and 2). Between births and/or expulsions of afterbirth, she often licked her pseudo-cloacal area. She also consistently licked her kits, either singly or all of them at a time, with no indication that any particular body area was more intensely treated than another. After ingesting a piece of afterbirth, she would thoroughly lick the floor, various parts of her own body and the neonates soiled with blood or fluids. It should be noted that virtually all of the licking behavior that we observed throughout our general study was performed by the female on parturition days (Patenaude and Bovet, in prep.).

In addition to the activities described above, the female displayed many other behaviors

that were part of her standard, non-parturient repertoire, such as self grooming, mutual grooming, feeding, wood-stripping, various types of vocalizations, sharpening teeth against each other, resting, dozing or sleeping. Compared to their displays in everday life, these activities were all brief suggesting restlessness in the female.

Male's and yearlings' behavior

In both years, the male and one yearling attended the whole process, forming with the female a triangular pen (Fig. 4) that enclosed the neonates. Yearling C was not seen at all in the lodge on the 1977 parturition day. By contrast, the two 1978 yearlings that were not part of the triangle remained in the lodge near the water hole, sleeping and grooming, until they left between the third and fourth births.

Fig. 3 (left). The female eats placenta while a kit makes unsuccessful attempts to suck. – *Fig. 4 (right).* The triangular pen. *Top right*: the female, licking a kit (in the center); *top left*: the yearling; *bottom*: the male

In 1977, formation of the triangle appeared to be a response to the moo-like vocalization of the female (see above). In 1978, it occurred in the observer's absence. Besides keeping the triangle closed (which presumably has a role in neonates' thermoregulation and protection), the male and a yearling exhibited behavior related to the kits. In 1977, after a neonate had managed to escape from the triangle and to fall into the water, the male got up, approached the water hole and then returned to his initial position once the kit had come back by itself. In 1978, the yearling licked the neonates on two occasions (Fig. 2).

Neonates' physical aspect and behavior

At delivery time, all young were covered with a dense, reddish-brown fur. Eyes were slightly open, incisors partially erupted and still covered with a thin membrane. Eyes were completely opened 2–4 hours after birth. Judging "by eye" (as well as from photographs), the neonates' size conformed to the standards found in the literature (see JENKINS and BUSHER 1979).

Within seconds from birth, kits began emitting sharp cries and whines and remained very vocal for the rest of the day. They also began to walk and climb with, at first, a certain lack of coordination. From their birth until the end of observation (see Figs. 1 and 2) many movements appeared to be attempts at reaching a nipple of the mother. They remained unsuccessful, however, because of the varied activities of the female (grooming, placentophagia, feeding, wood-stripping, etc.) in which she would not keep the appropriate posture for suckling (Fig. 3). First observation of effective sucking was made only later in the evening (at 20.50 in 1977 and at 20.30 in 1978). The kit that fell in the water hole was at most 3 hours old when this happened (Fig. 1). Whining, it swam for about 5 sec and climbed back to its siblings.

The radiographs of four full-term fetuses revealed a rudimentary stage of ossification. In the appendicular skeleton in particular, only the diaphysal part of the long bones was ossified. No ossification was found in the carpalia and, among tarsalia, only the calcaneum and astragalus exhibited some. This fully confirms the findings made by SCHINZ (1965) on a stillborn American beaver (see also photograph in HEDIGER 1970).

Movements into and out of lodge

In 1977, all seven beavers that attended parturition (female, male, yearling D and kits) fell asleep shortly before 17.00, at which time the observer left. When observations resumed at 19.50, only the male and the kits were in the lodge. The female reentered at 20.45. At 20.50, effective suckling was observed for the first time. Observations ended at 21.10, with both adults and the four kits but no yearlings in the lodge.

In 1978, one of the two yearlings that were not part of the protective triangle left the lodge at 15.48. The other followed soon after, returned, left and returned again and finally left without imminent return at 17.01. All these movements occurred between the third and fourth births, in a manner and at a time of day that were typical of normal daily routine at this time of year. The male left the lodge at 17.35, followed soon after by the yearling that was part of the triangle. The female then stayed alone with the kits for one more hour and left at 18.48, immediately after drinking water. Observations were then interrupted at 19.00 with the four kits alone in the lodge, sleeping since the female's departure. When observations resumed at 20.30, the female was nursing the kits with no other beaver present in the lodge. She left at 21.25 and, after 10 min of whining, the kits fell asleep. None of the older beavers reentered the lodge until the end of observation (22.55). However, they could be heard very close to the lodge, with many whines and hissings as well as occasional tail slaps. This was unusual behavior.

Discussion

In as far as they are comparable, our observations generally confirm and/or complete HEDIGER's (1970) findings, as well as the unpublished account of a parturition occurring in a bank-burrow observed by E. F. OERTLI (pers. comm.) on wild beavers in Western Canada. All stress the presence of the male and, facultatively, that of other members of the family in the nest during parturition. They feature the high amount of licking behavior displayed mostly by the female, both on herself and on the neonates. Also common to all

three sets of observations are the extreme rapidity of deliveries proper, the variability in interbirth intervals, the overall duration of the process and the expulsion of afterbirth in several fragments, which might reflect the structure of the uterus and the type of placentation in beavers (Fischer 1971; Gienc and Doboszynska 1972; Doboszynska 1978). Our observations, supported by Oertli's report, diverge from Hediger's with respect to the male's behavior: we found him to essentially play the passive role of a "pen-fence", with no attempts to eat placenta, lick the young or push them towards the female's teats. On the other hand, our observations have produced data on nest building or fitting activities related to parturition that fit well in the general features outlined above. With respect to placentophagia, it should be mentioned that our observations do not warrant, for beavers, the terms "avidity" or "enthusiasm" that have been used by Ewer (1968) and Kristal (1980) to characterize this behavior. Our female did eat placenta, but appeared to do it with some reluctance (see also Shadle 1930).

Generally speaking, Hystricomorphs are considered as typically precocial rodents, and Myomorphs or Sciurids as typically altricial. Establishing a distinction between precocial and altricial patterns related to parturition in beavers on the basis of a comparison with each of these types presents two kinds of difficulties. First, the accounts of parturition in either types are often fragmentary and/or possibly biased by keeping conditions. Second, there is some variability within a type: some Hystricomorphs are more precocial than others (Kleiman 1974), and the degree of altriciality is also variable among Myomorphs and Sciurids, a few species being even truly precocial (*Acomys cahirinus* and *A. russatus*: Dieterlen 1962; Porter and Doane 1978). Keeping this in mind, the following comments on precocial or altricial traits in beaver parturition are based on comparisons between our own observations and selected appropriate reports on either Hystricomorphs (Rood 1972; Kleiman 1972, 1974; Fulk 1976; Dubost and Genest 1974; Galef and Clark 1976) or Myomorphs (Rosenblatt and Lehrman 1963; King 1963; Ewer 1967; Blass and Teicher 1980) or Sciuromorphs (Cramblet and Ridenhour 1956; Prescott 1979). The physical external aspect of beaver neonates is typically precocial, and they display all major locomotory patterns, except diving, within a few minutes or at most hours from birth. Other traits that seem to be part of the precociality syndrom are the absence of licking aimed at the nipples (see Blass and Teicher 1980), the fact that the female does not isolate herself from the regular social group, and the direct contact of the neonates with older individuals other than the dam. On the other hand, the following could be considered akin to the altricial syndrome: the delivery posture with fetuses dropped in front of the mother (see Kleiman 1972), the fact that parturition occurs in the regular familial nest, and the prepartum nest-fitting activities. In addition, the degree of ossification at birth is typically altricial, being identical to that found in newborn mice *(Mus musculus)* or rats *(Rattus norvegicus)* and much less advanced than in newborn Guinea pigs *(Cavia porcellus)* (Curgy 1965). It should be noted that the altricial delivery posture might be imposed by the narrow space between floor and roof, and/or by the need to protect the fetus from falling into water at birth. Prepartum nest-fitting activities are definitely common in the altricial syndrome, yet are also present in a few precocial species. For instance, Fulk (1976) described in *Octodon degus* a prepartum transport of grass into burrows performed by both females and males. Interestingly, this species is in other respects less precocial than other Hystricomorphs (Kleiman 1974). Concerning the "altricial" degree of ossification, it is perhaps related to the confinement of the kits in the lodge for 4–5 weeks (see Patenaude on ontogeny, in prep.). It is of comparative interest that hare neonates (genus *Lepus*), that are considered as definitely precocial animals (Bourlière 1951), have the same rudimentary state of ossification as their typically altricial relative, the rabbit *(Oryctolagus cuniculus)* (Petri 1935, cited by Curgy 1965).

It appears therefore impossible to assess beaver parturition and related phenomena as a whole to either term of the antinomy precociality vs. altriciality. Rather, they are

characterized by a complex mosaic of elements that belong to either one or the other category.

Acknowledgements

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Zusammenfassung

Die Geburt bei freilebenden Kanadabibern (Castor canadensis)

In zwei aufeinanderfolgenden Jahren wurde bei einer Familie freilebender Kanadabiber *(Castor canadensis)* die Geburt in der Burg beobachtet. Das Verhalten der Familienangehörigen, der Eltern, der insgesamt fünf Einjährigen und acht Neugeborenen, vor und während der Geburt und die Morphologie der Neugeborenen werden beschrieben und mit den bei Bibern in Gefangenschaft gewonnenen Beobachtungen verglichen. In Verhalten und Morphologie vereinen Biber Merkmale, die teils für Nesthocker, teils für Nestflüchter bezeichnend sind. Die Biber können daher keinem der beiden Typen vorbehaltlos zugeordnet werden.

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Altersbedingte Veränderungen am lymphatischen System der Rötelmaus *(Clethrionomys glareolus)*

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Abstract

Age-dependent variations in the lymphatic system of Clethrionomys glareolus

Studied were the distribution and frequency of alkaline phosphatase-positive lymphocytes in the peripheral blood and lymph node of 46 *Clethrionomys glareolus* for different ages. With increasing age there was a striking depletion of alkaline phosphatase-positive lymphocytes, which in this species represent the T lymphocyte subclass. The age-dependent reduction of enzyme-positive lymphocytes was particularly noticeable in the peripheral blood and lymphatic organs. In addition to the methods already available for age determination (length of the root of the 1st molar, vertebral body index), the frequency of alkaline phosphatase-positive lymphocytes in the peripheral blood represents a new tool for age determination in this species.

The diminution of T lymphocytes with increasing age supports the hypothesis of those authors who attribute a relevant life-limiting factor to the declining thymus function.

The age-dependent lymphocyte depletion correlates very well with the newly developed technique for age evaluating, i.e. the length of four following coccygeal vertebra in the proximal region.

Einleitung

In der freien Natur hängt die Lebenserwartung von Kleinsäugern von zahlreichen endo- und exogenen Faktoren ab. Bei den exogenen Einwirkungen sind vor allem Witterungseinflüsse, die Zahl der natürlichen Feinde, die Quantität und Qualität des Futters und die

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